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Correction to ‘Trait evolution, resource specialization and vulnerability to plant extinction samong Antillean hummingbirds’

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Trait evolution, resource specialisation and vulnerability to plant extinctions among Antillean hummingbirds

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Abstract (max 200 words)

Species traits are thought to predict feeding specialisation and the vulnerability of a species to extinctions of interaction partners, but the context in which a species evolved and currently inhabits may also matter. Notably, the predictive power of traits may require that traits evolved to fit interaction partners. Furthermore, local abiotic and biotic conditions may be important. On islands, for instance, specialised and vulnerable species are predicted to be found mainly in mountains, whereas species in lowlands should be generalized and less vulnerable. We evaluated these predictions for hummingbirds and their nectar-food plants on Antillean islands. Our results suggest that the rates of hummingbird trait divergence were higher among ancestral mainland forms before the colonization of the Antilles. In correspondence with the limited trait evolution that occurred within the Antilles, local abiotic and biotic conditions – not species traits – correlate with hummingbird resource specialisation and the vulnerability of hummingbirds to extinctions of their floral resources. Specifically, hummingbirds were more specialised and vulnerable in conditions with high topographical complexity, high rainfall, low temperatures, and high floral resource richness, which characterize the Antillean Mountains. These findings show that resource specialisation and species vulnerability to extinctions of interaction partners are highly context dependent.

Keywords: island biology, mountains, mutualistic networks, endemics, specialisation, taxon cycles

1. Introduction

For more than one hundred and fifty years, ecologists have realized that species are entangled in networks of interactions with locally co-occuring species [1, 2]. Species interaction networks can be used to investigate whether species traits influence resource specialisation and species vulnerability to extinctions of their interaction partners [3–5], but how these crucial aspects of species ecology are predicted by local abiotic and biotic conditions is less well known [6–8]. Moreover, although traits may evolve to exploit specific resources and minimize competition [9, 10], it is poorly understood whether the importance of traits in determining resource specialisation and species vulnerability is related to rates of trait evolution. In other words, the context in which a species evolved, and is currently distributed, is often neglected as a determinant of resource specialisation and vulnerability to the extinction of interaction partners.

With respect to resource specialisation, island organisms are often found to be more generalized than their mainland counterparts, and sometimes engage in interactions rarely observed on the mainland e.g. pollination by lizards [11–13]. Such generalized behavior may be due to the limited number of species and reduced interspecific competition on islands, resulting in ecological release and the evolution of generalized feeding niches [11]. Colonization history may also matter, as mainland generalists from the lowland should more easily colonize and establish on islands than mainland specialists and mountainous species [14, 15]. However, not all island species have generalized feeding niches, particularly if they undergo sequential phases of range expansion and contraction as predicted by taxon cycle theory. Notably, according to taxon cycle theory, newly colonized species that are in a period of range expansion often have fairly generalized niches and establish in marginal lowland habitats, whereas species at the end of the taxon cycle are endemics specialised to interior mountain abiotic and biotic environments [15–17]. Thus, contrary to the prevailing trend for island species to be generalists, mountain endemics may provide extreme

examples of specialisation. One such example is the Purple-throated Carib (*Eulampis jugularis*), an endemic hummingbird specialised to feed on nectar from the flowers of *Heliconia* plants in the Lesser Antillean mountains [9, 18]. On islands, there should therefore be an association between local conditions and the level of resource specialisation: lowland species being generalized and species in mountains being more specialised.

In addition to these geographical trends in resource generalization-specialisation, island species are known to be more vulnerable to extinction than mainland species [19, 20]. For example, during the last 400 years, about 90% of all bird extinctions have occurred on islands [19]. This is thought to be a consequence of island populations being small – many are endemic to one or a few islands – and because island species have evolved largely in isolation. Thus, species on islands are susceptible to natural disasters, habitat destruction and introduced species [20], such as rats or cats, causing extinctions and threatening endemics across numerous islands throughout the world. The negative consequences of disrupting mutualistic associations are a further potentially important influence upon the extinction risk of island taxa, but these are less well known [21]. Bird pollination provides a good example of how disrupting mutualistic associations can influence reproductive output and population density [22]. Recently, species vulnerability to the extinction of their mutualistic partners has been modelled using networks of interactions between animal and plant communities [5, 7, 23, 24], illustrating that plant extinctions are more likely to cause animal coextinctions than *vice versa* [7]. However, it remains poorly understood how animal vulnerability to plant extinctions is affected by their traits and local abiotic and biotic conditions.

Here, we use mutualistic plant-hummingbird networks in the Antillean archipelago to ask how species traits and local abiotic and biotic conditions relate to resource specialisation and hummingbird vulnerability to plant extinctions. Hummingbirds have a long co-evolutionary history with their nectar-food plants, which they are energetically highly dependent on. Likewise, although

plants pollinated by hummingbirds may also be pollinated by other animals [18], many are, to a large extent, dependent on hummingbird's pollination services [25, 26]. Notably, large-bodied and long-billed hummingbirds, and those living in wet, cool and topographically heterogeneous environments, seem to establish specialised interactions with their nectar-food plants [9, 18, 27–29]. High resource specialisation may reduce competition between hummingbirds, increase the likelihood of pollen transfer among conspecific plants [3, 30], and thus benefit both the hummingbirds and their nectar-food plants. However, high resource specialisation may also make them more vulnerable to extinctions of their mutualistic partners [31, 32]. It is therefore important to understand to what degree resource specialisation and vulnerability to plant extinctions are associated with hummingbird traits and local abiotic and biotic conditions. As the evolution of hummingbird traits, notably bill length and body mass, may be associated with specialisation on specific floral resources that have matching corolla morphologies and nectar-production rates [9], it is relevant to assess the degree of trait evolution among the Lesser Antillean hummingbirds. As such, we expect hummingbird traits to determine specialisation and vulnerability when traits have co-evolved *in situ* to fit their floral partners in the Antilles. Thus we ask: (1) have the rates of hummingbird body size and bill length evolution been highest early or late in the history of Antillean hummingbirds, i.e. did hummingbird body size and bill length evolve primarily among ancestral mainland forms prior to colonizing the islands or more recently on the Antillean islands? (2) within the Antilles, is hummingbird resource specialisation and vulnerability to plant extinctions associated mainly with (a) morphological traits that are important for partitioning floral resources, i.e. hummingbird bill length and body mass, or (b) the abiotic and biotic conditions of the localities in which they occur? As measures of local abiotic conditions we include topographic heterogeneity, precipitation, and temperature, whereas biotic conditions were represented by hummingbird and nectar-food plant richness. These abiotic and biotic factors are hypothesized to influence how

hummingbirds partition floral resources. Specifically, species-rich communities and wet, cool mountain environments are hypothesized to support more specialised and vulnerable hummingbird species [18, 27].

2. Materials and Methods

(a) Hummingbird trait evolution

Extant hummingbirds colonised South America ~ 22 Mya, and arrived through multiple colonization events to the Antillean archipelago approximately 5-9 Mya (Figure 1a, [33, 34]). All Antillean hummingbirds are endemic to the archipelago, except the Rufous-breasted Hermit (*Glaucis hirsutus*) which is found both on the South American mainland and on Grenada, the most southern island of the Antilles. We used phylogenetic comparative methods to evaluate changes in the rate of morphological evolution among Antillean hummingbird species through time, and to subsequently assess whether the body size and bill length of Antillean hummingbirds likely evolved on the mainland prior to colonizing the islands, or on the Antillean islands. To achieve this, we used a recent hummingbird phylogeny [33] which represents a highly resolved time-calibrated analysis of molecular data from 284 hummingbird species (~86% of all hummingbird species). The maximum clade credibility tree from this analysis was pruned to contain 13 of the 14 Antillean hummingbird species. Among the Antillean species, only *Mellisuga helenae* is missing from the phylogeny [33]. We analyzed rates of hummingbird morphological diversification using phylogenetic independent contrasts (PICs; [35]) and Blomberg's K in the R packages APE and phytools [36–38]. The absolute values of the contrasts for body mass and bill length were regressed against node age using linear models, which enables assessment of how evolutionary rates change through time. Subsequently, we used Blomberg's K to test for the phylogenetic signal in both body

158 mass and bill length. PICs and Blomberg's K represent alternative methods of assessing rates of
159 trait evolution and how these compare to the null expectation under a Brownian motion model of
160 evolution [35–38]. The smallest bird in the world, the Bee Hummingbird (*Mellisuga helenea*), is
161 endemic to Cuba in the Greater Antilles. Although *Mellisuga helenae* is missing from the
162 phylogeny [33], and therefore not included in our analysis, we expect the results presented to be
163 robust to the inclusion of this species given the similarity in body mass and bill length with its
164 congener *Mellisuga minima* (2.2 g *versus* 2.4 g body mass; 10.8 mm *versus* 10.5 mm bill length;
165 Table S1).

166 **(b) Hummingbird specialisation on nectar-food plants**

167 To estimate hummingbird specialisation on nectar-food plants in the Antilles, we assembled a
168 database of our own Antillean hummingbird-plant network studies, which recorded mutualistic
169 interactions between assemblages of hummingbirds and their nectar-food plants. Details on the
170 sampling can be found in [18], but here we give a brief overview. The database includes eight
171 networks covering 12 of the 14 hummingbird species in the Antilles, only missing the Jamaican
172 Mango (*Anthracothorax mango*) and Hispaniolan Emerald (*Chlorostilbon swainsonii*). Within the
173 study plots of each network, we surveyed all flowering plant species for hummingbird visitation. In
174 all networks, the link weight of each legitimate plant-hummingbird interaction was reported as the
175 visitation rates of hummingbirds to flowers. Compared to binary networks, which only record
176 whether an interaction occurred or not, weighted networks better reflect the dependencies between
177 species [39]. Additionally, network-derived specialisation indices based on weighted networks are
178 less sensitive to sampling effort than their binary counterparts, making cross-network comparisons
179 more reliable [40–43]. All studies collected hummingbird-plant interactions within the same season
180 (March to July) and approximately the same sampling length (1.5 to 3.5 months; mean 3 months).
181 The size of the study plots were: 200 m x 5 m (Cuba, Puerto Rico, Grenada; 5 plots), 400 m x 5 m

(Dominica; 2 plots) and 870 m x 6 m (Jamaica; 1 plot). In every study, we observed all hummingbird species whose range distribution overlapped the study area. The raw quantitative hummingbird-plant networks can be downloaded from Dryad (doi:10.5061/dryad.5770gm7). See Supplementary material Table S1 for details on the local abiotic and biotic conditions of each network: topographic heterogeneity, precipitation, temperature, and richness of hummingbirds and nectar-food plants.

To estimate hummingbird specialisation, we used the 'complementary specialisation' metric, which is a measure of the partitioning of interactions among species in weighted networks [40]. We calculated the species-level version of complementary specialisation *d'* (Kullback–Leibler divergence), which measures the interaction specialisation of a given species by quantifying the deviation of interaction frequencies from a null expectation that assumes that all partners interact proportionally to their availability, using interaction frequency as a surrogate for abundance [40]. Values of *d'* are scaled to range from 0 to 1 indicating the extremes of generalization and specialisation, respectively. Complementary specialisation *d'* is conceived to account for differences in species richness among networks [40]. Calculations of hummingbird specialisation *d'* were conducted in the bipartite package 1.20 in R [38, 44].

Next, we used linear mixed effects models to examine how hummingbird specialisation *d'* associates with local conditions (abiotic: topography, temperature, precipitation; and biotic: richness of hummingbirds and plants, i.e. network size) and hummingbird traits (bill length and body mass). First, however, due to the relatively small sample size (n = 12 hummingbird species) and large number of intercorrelated variables (e.g. for hummingbird bill length and body mass: n = 12 species, r = 0.87, P < 0.05), we reduced the number of predictor variables to two using Principal Component Analysis (PCA). To do this, for each of the two groups of predictors (local conditions and species traits), we used PCA and the broken stick method, identifying one PCA axis

each for local conditions (explaining 69% of the total variation; loading: temperature = -0.607, precipitation = 0.832, topography = 0.941, network size = 0.894) and species traits (95%; loading: bill length = 0.975, body mass = 0.975). We note that the data are suitable for PCA analysis, being approximately linear, homoscedastic and normally distributed (- 1.0 < skewness < 1.1 [45]). The resulting PCA axes were likewise suitable for linear mixed effects modelling and were not correlated ($r = 0.174$; $p > 0.05$), i.e. there was no association between the local conditions and hummingbird traits. We then ran two linear mixed effects models, one for each of the PCA axes as fixed effects, to predict hummingbird specialisation *d'*. We used linear mixed effects models because three hummingbird species were observed in more than one network (Table S1) and, therefore, we included hummingbird species identity as a random factor to account for the non-independence of the observations of the same species occurring in different networks [6, 46]. We also ran a full model including both PCA axes (local conditions and hummingbird traits) as predictors of hummingbird specialisation *d'*. Finally, we performed a set of supplementary models, analyzing the association between hummingbird specialisation *d'* and the three components of local conditions: 1) local abiotic conditions, 2) local floral resource richness, and 3) local hummingbird richness (the latter two factors representing local biotic conditions). To do this, we first used PCA and the broken stick method for the local abiotic conditions, identifying one PCA axis (explaining 68% of the total variation; loading: temperature = -0.681, precipitation = 0.849, topography = 0.920). This axis was strongly positively correlated with local resource plant richness ($r = 0.721$; $p < 0.05$), indicating that in the Antilles there are more hummingbird-visited plant species in topographically complex, high precipitation and low temperature localities than in topographically simple, drier and warmer areas [18, 47]. There was no association between the size of the study plots, the length of the sampling period and the floral resource richness within each site (study plot size: $n = 8$ sites, Pearson's $r = -0.141$; $p = 0.74$; sampling period: $n = 8$ sites, Pearson's $r = 0.187$; $p =$

0.66), or with hummingbird specialisation (study plots: R^2 marginal = 0.01, R^2 conditional = 0.01; p = 0.68; sampling period: R^2 marginal = 0.12, R^2 conditional = 0.12; p = 0.16).Thus neither the different sizes of the study plots nor differences in the sampling periods influence our results. For all linear mixed effects models, we report AIC_c, marginal R^2, and conditional R^2 values to evaluate model performance. To evaluate the performance of each predictor variable, we report coefficient estimates and corresponding P-values, standard errors and 95% confidence intervals. The PCA analyses were conducted in SAM 4.0 [48] and the linear mixed models in SPSS 22 [49].**(c) Hummingbird vulnerability to plant extinctions**

We assessed the vulnerability of hummingbird species to iterative plant extinctions in the networks using the recently developed Stochastic Coextinction Model (SCM), full details of which can be found in [50]; here we give a brief overview. In the model, $P_{ij} = R_i d_{ij}$ is the probability of species *i* going extinct following the extinction of its partner species *j*. R_i is a species-level property between 0 and 1 that reflects the intrinsic demographic dependence of *i* on the pollination mutualism. In this study, where species *i* is a plant, R_i reflects the plant's dependence on hummingbird pollination. Where species *i* is an animal, R_i reflects hummingbird dependence on floral nectar. d_{ij} is the dependence of *i* on *j*, defined as the interaction strength between *i* and *j* divided by the total interaction strength between *i* and all its mutualistic partners. In the SCM, let A and B be the two sets of species in the network, with A representing plant species and B representing hummingbird species. Simulations start with the extinction of a single plant species in A. Next, all hummingbird species in B have a probability of extinction following the equation $P_{ij} = R_i d_{ij}$. For each extinction in B, if any, all species in A have a probability of extinction, and so on. This process continues until there are no extinctions and equilibrium is reached. In this way, the SCM allows for complex coextinction cascades: a plant extinction can lead to a pollinator extinction, which in turn can lead to a plant extinction, and so forth. A pervasive phenomenon in nature is the ability for pollinators to

rewire, i.e. compensate for the loss of a partner plant species by reallocating lost interactions to other species in the community [51]. In this respect, it is also important to note that, in the SCM, a given species may survive even if all of its partners become extinct, reflecting that hummingbirds may be able to switch to other food resources and plants may not only be pollinated by hummingbirds [18]. Therefore, simulating species vulnerability to extinction using mutualistic networks may not reflect real extinctions in nature, but should reflect reduction in fitness. It is thus an appropriate tool to understand which species are most vulnerable to extinction of their mutualistic partners [24].

We ran two groups of simulations. In the first group ('random plant *R* values'), *R* values for plants were sampled from a uniform distribution between 0 and 1, with all plant species being assigned the same *R* value in each model run [50]. In the second group ('expert-assigned plant *R* values), *R* values for plants were assigned based on expert opinion using fieldwork knowledge on floral phenotype and known insect visitation, which may contribute to pollination of hummingbird-visited flowers [18]. Each plant species was assigned low (0 – 0.33), medium (0.33 – 0.66) or high (0.66 – 1) *R* values, or values spanning two or more of these categories. Plants assigned as 'low' have flowers pollinated by both hummingbirds and insects; plants scored as 'medium' were plants with intermediate dependence on pollination by hummingbirds; 'high' categorized plants have ornithophilous syndrome flowers rarely visited by insects (for details, see Supplementary Table S2). In each run, all 'low' species were assigned the same randomly sampled value in the 'low' range, all 'medium' species were assigned the same randomly sampled value in the 'medium' range etc. In both group of simulations, as hummingbirds are highly dependent on floral nectar, *R* values for hummingbirds were assigned as 'high' (0.66 – 1). In each run, all hummingbird species were assigned the same randomly sampled value in the 'high' range. For both groups of model runs (random plant *R* values and expert-assigned plant *R* values), we carried out

three sets of simulations, corresponding to three different plant extinction sequences [5, 24]. In the first set of simulations, we iteratively removed the lowest degree plant species, i.e. those plant species with fewest hummingbird pollinators. This represents a 'realistic extinction scenario' as specialist species tend to be more vulnerable to extinction [24, 31, 32]. In the second set of simulations, we iteratively removed the highest degree species. This quantifies the 'attack tolerance' of the network; a 'worst case scenario' where high degree nodes are lost first [52, 53]. Finally, we simulated the loss of plants in a random order: this represents the null expectation between the two systematic removal orders discussed above [24]. All simulations were run 10,000 times.

From these six simulations (two methods of assigning plant *R* values and three plant extinction sequences), we calculated three measures of hummingbird vulnerability to plant extinctions: (i) the probability of extinction, *PE*, defined as the proportion of the 10,000 runs in which the species went extinct; (ii) the average proportion of plant species which had to be removed for a given hummingbird species to go extinct across the 10,000 runs (excluding model runs when it survived), representing the speed of extinction, *SE*; and (iii) a novel index of vulnerability of extinction, *VE*, where $VE = PE\,(1 - SE)$. This index captures two components of vulnerability, such that species are considered more vulnerable when they have a higher probability of extinction (*PE*) and when, on average, their extinction occurs early in an extinction sequence (when $1 - SE$ is high). The R-codes for calculating the three measures of vulnerability can be downloaded from Dryad (doi:10.5061/dryad.5770gm7).

We examined the association between the three measures of hummingbird vulnerability (*PE*, *SE*, and *VE*) and local conditions (temperature, precipitation, topography, and network size, i.e. species richness of hummingbirds and plants) and hummingbird traits (bill length and body mass) using linear mixed effects models. In all cases, the calculations were performed for all three extinction scenarios (iteratively removing species with the lowest degree; iteratively

removing species with the highest degree, removing species at random), and for both methods of assigning plant *R* values: random (Tables 2, S4, S7) and expert assigned dependency values based on floral phenotype and insect visitation (Tables S5-S6). The linear mixed effects modelling approach was identical to the one for hummingbird specialisation *d'*, including the use of PCA axes, except in this instance we used hummingbird vulnerability as the response variable. We report the results both for the 'Index of vulnerability', *VE*, (Tables 2, S5 and S7), and 'the speed of extinction', calculated as 1 – *SE*, (Tables S4 and S6). As we forced the networks to collapse completely in terms of simulating the removal of all plant species (see above), the probability of hummingbird extinction *PE* was very high for nearly all species ($0.83 < PE < 0.98$), thus *PE* showed no association to either local conditions or to hummingbird traits (results not shown).

3. Results

(a) Hummingbird trait evolution

The absolute contrast values of bill length showed a significant negative correlation with distance from the root of the phylogeny (Figure 1b; $r = -0.87$, $P < 0.001$), indicating higher rates of morphological evolution early in the history of Antillean hummingbirds, which has subsequently slowed towards the present day. Differences in hummingbird bill length appear to have accumulated mainly before the colonization of the Antilles 5-9 Mya (Figure 1b). Blomberg's K indicated a greater amount of evolution in bill length than expected under Brownian motion ($K = 1.65$; $P = 0.001$) and thus species that share recent evolutionary history are more similar in bill length than expected by chance. Conversely, body mass contrasts were positively but non-significantly correlated with distance from the root of the tree (Figure 1c; $r=0.28$, $P= 0.38$). Blomberg's K suggested body mass to be more divergent than expected under Brownian motion, however, this phylogenetic signal was also non-significant upon performing a randomization test ($K = 0.41$, $P =$

0.21). These results suggest the lack of a general trend in the evolution of body mass through time among Antillean hummingbirds; however, we note a large recent contrast among congeners of the genus *Eulampis*, which is endemic to the Antilles (Figure 1c).

(b) Hummingbird specialisation on nectar-food plants

The specialisation of hummingbirds on their nectar plants was not significantly associated with hummingbird body mass or bill length (Table 1). Instead, hummingbird specialisation was strongly associated to the local conditions (Table 1), with specialisation increasing as a factor of the local abiotic conditions (high topographic complexity, high precipitation, and low temperature promoting specialisation; Table S3, Figure 2a) and hummingbird and floral resource richness (Table S3, Figure 2b).

(c) Hummingbird vulnerability to plant extinctions

The vulnerability of hummingbirds to plant extinctions *VE* was not associated with the morphological traits analysed: small and large bodied/billed hummingbirds were equally vulnerable (Table 2, S5). Instead, when removing plant species in a 'realistic extinction scenario' (iteratively removing lowest degree plant species) and at random, hummingbird vulnerability was strongly associated to the local conditions (Table 2): hummingbirds were most vulnerable in conditions characterized by high topographic complexity, high precipitation, low temperature, and high floral resource richness (Figure 2c, d). The 'attack tolerance' of the network (iteratively removing highest degree plant species) showed no association to either hummingbird traits or local conditions. The results were qualitatively similar when vulnerability was modelled using the speed of hummingbird extinctions 1 – *SE* (Tables S4, S6). All results were also qualitatively consistent irrespective of whether plant dependencies on hummingbird pollination, *R*, were assigned randomly or by expert opinion (Tables 2, S4-S6).

4. Discussion

Our results suggest that high rates of divergence in hummingbird bill length primarily occurred before lineages colonised the Antilles approximately 5-9 Mya, while the evolution of body mass differences were more constant through time (Fig. 1). In correspondence with the limited trait evolution occurring within the Antilles, especially bill length that have often been shown to determine floral niche partitioning [420, 542], we found that hummingbird specialisation on floral resources and their corresponding vulnerability to plant extinctions were not predicted by their bill length and body mass. Instead, hummingbird resource specialisation and vulnerability to plant extinctions were strongly associated with high topographical complexity, more rainfall, cooler temperatures, and greater richness of flowers utilised by hummingbirds (Fig. 2), conditions which characterize the Antillean Mountains [18, 47].

These findings fit well with expectations of taxon cycle theory, which predicts that endemic species found in interior mountains are specialised and vulnerable species, whereas species in the lowlands are more generalized and resilient [15, 16]. The repeated structuring of Antillean hummingbird communities into lowland and highland communities – each consisting of one small and one large bodied/billed species – has been suggested to be a consequence of competition, possibly for floral resources [14, 55]. Similar patterns have been observed for other pollination systems, such as coexisting bumblebees that differ in proboscis length to minimize competition [56]. For Antillean hummingbirds, there is also recent evidence of competitive exclusion, as the Lesser Antillean species *0rthorhyncus cristatus* and *Eulampis holosericeus* have expanded north in recent years displacing the Greater Antillean species *Anthracothorax dominicus* from many of the Virgin Islands and northeastern Puerto Rico [14, 57]. Combined with the apparently limited trait

372 evolution that occurred in the Antilles (Fig. 1), this suggests that the structuring of hummingbird
373 communities largely reflects an assembly process, possibly driven by competition for the limited
374 nectar-food plant richness observed in the Antilles. The competition for floral resources may have
375 allowed hummingbirds already differentiated in size, i.e. only one small and one large bodied/billed
376 hummingbird species, to enter a given community, thereby resulting in minor evolutionary changes
377 in bill length and body mass among the constituent Antillean hummingbird species. This idea is
378 similar to Janzen's 'ecological fitting' hypothesis, whereby species utilize niches based on the traits
379 they carried with them but which evolved somewhere else [58, 59]. The main exception to this
380 general trend was a large divergence in body mass between the members of the genus *Eulampis*
381 (Fig. 1c). We suggest this most likely reflects evolutionary increases in the mass of *Eulampis*
382 *jugularis*, a large and highly dimorphic mountain endemic that is highly specialised on *Heliconia*
383 flowers [9, 18]. Conversely, *E. holosericeus* is a smaller and less dimorphic species feeding on an
384 array of flowers throughout the Lesser Antillean lowlands [18]. This would further underline that
385 the Antillean mountains has provided optimal conditions for specialised associations between
386 hummingbirds and their nectar-food plants.

387 Taken together, our results indicate that mountain environments, and the
388 corresponding high richness of flowering plants attracting hummingbird pollinators, have
389 influenced the evolution and maintenance of a highly specialised and vulnerable endemic
390 hummingbird fauna in the Antillean Mountains. These results have implications for the
391 conservation of species engaged in mutualistic associations. Notably, as climate change and
392 anthropogenic activity disrupt mutualistic associations, and cause pollinator and plant extinctions
393 [7, 60, 61], the montane biota of the Antilles is more susceptible to extinction of mutualistic
394 partners than the biota in the lowlands. The role of mountain environments in sustaining a highly
395 specialised and vulnerable endemic fauna may be a general phenomenon also occurring in other

taxa and in a mainland context [29, 62]. This underlines that resource specialisation and vulnerability is highly context dependent, and that the local abiotic and biotic conditions should be more integrated into studies predicting resource specialisation and vulnerability to extinctions of interaction partners.

Data accessibility

The raw quantitative hummingbird-plant networks, morphological and phylogentic data can be downloaded at Dryad (doi:10.5061/dryad.5770gm7). For each hummingbird-plant network, details on the local abiotic and biotic conditions, i.e. temperature, precipitation, topography, and richness of hummingbirds and their nectar-food plants, is presented in the electronic supplementary material, table S1. In table S1, for each hummingbird species, we also give its body mass, bill length, and network-derived estimates of resource specialization *d'* and vulnerability *VE*. Assigned *R* values for plants based on expert opinion, using knowledge on floral phenotype and known insect visitation [18], are available in Table S2.

Authors' contributions

B.D. designed the study, conducted the mixed models analysis, and wrote the manuscript. J. K. conducted the phylogenetic analysis. B.I.S conducted the plant extinction analysis. A.M.M.G conducted the network analysis. A.C.B, A.M.M.G. and A.T. contributed plant-hummingbird networks. All authors contributed to interpretation of the data and manuscript writing.

Competing interests

We have no competing interests.

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References

1. Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London, UK: John Murray.
2. Montoya, JM, Pimm, SL, Solé, RV. 2006 Ecological networks and their fragility. *Nature* **442**, 259–264. (doi:10.1038/nature04927)

436 3. Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M. 2014 Morphological traits
437 determine specialization and resource use in plant–hummingbird networks in the neotropics.
438 *Ecology* **95**, 3325-3334. (doi:10.1890/13-2261.1)

439 4. Dehling, DM, Jordano, P, Schaefer, HM, Böhning-Gaese K, Schleuning, M. 2016
440 Morphology predicts species' functional roles and their degree of specialization in plant–
441 frugivore interactions. *Proc R Soc B* **283**, 20152444. (doi: 10.1098/rspb.2015.2444)

442 5. Memmott J, Waser NM, Price MV. 2004 Tolerance of pollination networks to species
443 extinctions. *Proc R Soc B* **271**, 2605–2611. (doi:10.1098/rspb.2004.2909)
444 6. Maruyama, PK et al. 2016 The integration of alien plants in mutualistic plant–hummingbird
445 networks across the Americas: the importance of species traits and insularity. *Divers Distrib*
446 **22**, 672–681. (doi:10.1111/ddi.12434)
447 7. Schleuning M et al. 2016 Ecological networks are more sensitive to plant than to animal
448 extinction under climate change. *Nat commun* **7**, 13965. (doi:10.1038/ncomms13965)

449 8. Tinoco BA, Graham CH, Aguilar JM, Schleuning M. 2017 Effects of hummingbird
450 morphology on specialization in pollination networks vary with resource availability. *Oikos*
451 **126,** 52–60. (doi:10.1111/oik.02998)
452 9. Temeles EJ, Kress J. 2003 Adaptation in a plant-hummingbird association. *Science* **300**,
453 630–633. (doi:10.1126/science.1080003)
454 10. Grant, PR, Grant, BR. 2006 Evolution of character displacement in Darwin's finches.
455 *Science* **313**, 224–226. (doi: 10.1126/science.1128374)
456 11. Olesen JM, Eskildsen LI, Venkatasamy S. 2002 Invasion of pollination networks on oceanic
457 islands: importance of invader complexes and endemic super generalists. *Divers Distrib* **8**,
458 181–192. (doi:10.1046/j.1472-4642.2002.00148.x)

12. Olesen JM, Valido A. 2003 Lizards as pollinators and seed dispersers: an island phenomenon. *Trends Ecol Evol* **18**: 177–181. (doi:10.1016/S0169-5347(03)00004-1)
13. Dalsgaard, B, Baquero, AC, Rahbek, C, Olesen, JM, Wiley, JW. 2016. Speciose opportunistic nectar-feeding avifauna in Cuba and its association to hummingbird island biogeography. *J Ornithol* **157**, 627–634. (doi:10.1007/s10336-016-1326-6)
14. Lack D. 1973 The number of species of hummingbirds in the West Indies. *Evolution* **27**, 326–337. (doi:10.2307/2406972)
15. Ricklefs RE, Cox GW. 1972 Taxon cycles in the West Indian avifauna. *Am Nat* **106**, 195–215.
16. Wilson EO. 1961 The nature of the taxon cycle in the Melanesian ant fauna. *Am Nat* **95**, 169–193.
17. Ricklefs, R. E. and Bermingham, E. 2002 The concept of the taxon cycle in biogeography. *Glob Ecol Biogeogr* **11**, 353–361. (doi:10.1046/j.1466-822x.2002.00300.x)
18. Dalsgaard, B, Martín González, AM, Olesen, JM, Ollerton, J, Timmermann, A, Andersen, LH, Tossas, AG. 2009 Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. *Oecologia* **159**, 757–766. (doi:10.2307/40309943)
19. Johnson, TH, Stattersfield AJ. 1990 A global review of island endemic birds. *Ibis* **132,** 167–180. (doi:10.1111/j.1474-919X.1990.tb01036.x)
20. Blackburn, TM, Cassey, P, Duncan, RP, Evans, KL, Gaston, KJ. 2004 Avian Extinction and Mammalian Introductions on Oceanic Islands. *Science* **305**, 1955-1958. (doi:10.1126/science.1101617)

481 21. Kaiser-Bunbury, CN, Traveset, A, Hansen, DM. 2010 Conservation and restoration of
482 plant–animal mutualisms on oceanic islands. *Perspect Plant Ecol Evol Syst* **12**, 131–143.
483 (doi:10.1016/j.ppees.2009.10.002)
484 22. Anderson SH, Kelly D, Ladley JJ, Molloy S, Terry J. 2011 Cascading effects of bird
485 functional extinction reduce pollination and plant density. *Science* **331**, 1068–1071.
486 (doi:10.1126/science.1199092)
487 23. Kaiser-Bunbury, CN, Muff, S, Memmott, J, Müller, CB, Caflisch, A. 2010 The robustness
488 of pollination networks to the loss of species and interactions: a quantitative approach
489 incorporating pollinator behavior. *Ecology Letters* **13**, 442–452. (doi: 10.1111/j.1461-
490 0248.2009.01437.x)
491 24. Dáttilo, W, Lara-Rodríguez, N, Jordano, P, Guimarães, PR Jr, Thompson, JN, Marquis, RJ,
492 Medeiros, LP, Ortiz-Pulida R, Marcos-García, MA, Rico-Gray, V. 2016 Unravelling
493 Darwin's entangled bank: architecture and robustness of mutualistic networks with multiple
494 interaction types. *Proc R Soc B* **283**, 20161564. (doi:10.1098/rspb.2016.1564)
495 25. Feinsinger P, Colwell RK. 1978 Community organization among neotropical nectar-feeding
496 birds. *Am Zool* **18**, 779–796.
497 26. Stiles FG. 1978 Ecological and evolutionary implications of bird pollination. *Am Zool* **18**,
498 715–727.
499 27. Dalsgaard, B. et al. 2011 Specialization in plant-hummingbird networks is associated with
500 species richness, contemporary precipitation and quaternary climate-change velocity. *PLoS*
501 *One* **6**, e25891. (doi:10.1371/journal.pone.0025891)
502 28. Martín González AM et al. 2015 The macroecology of phylogenetically structured
503 hummingbird-plant networks. *Glob Ecol Biogeogr* **24**, 1212–1224. (doi:10.1111/geb.12355)

504 29. Sonne J et al. 2016 High proportion of smaller ranged hummingbird species coincides with
505 ecological specialization across the Americas. *Proc R Soc B* **283**, 20152512.
506 (doi:10.1098/rspb.2015.2512)
507 30. Brosi, BJ, Briggs, HM. 2013 Single pollinator species losses reduce floral fidelity and plant
508 reproductive function. *Proc Natl Acad Sci USA* **110**, 13044–13048.
509 (doi:10.1073/pnas.1307438110)

510 31. Olesen JM, Jain SK. 1994 Fragmented plant populations and their lost interactions. In
511 Conservation genetics (ed. V. Loeschcke, J. Tomiuk & S. K. Jain), pp. 417–426. Basel:
512 Birkhäuser.

513 32. Bond WJ. 1995 Assessing the risk of plant extinction due to pollinator and disperser failure.
514 In Extinction rates (ed. J. H. Lawton & R. M. May), pp. 131–146. Oxford University Press.

515 33. McGuire JA, Witt CC, Remsen Jr JV, Corl A, Rabosky DL, Altshuler DL, Dudley R. 2014
516 Molecular phylogenetics and the diversification of hummingbirds. *Curr Biol* **24**, 910–916.
517 (doi:10.1016/j.cub.2014.03.016)

518 34. Abrahamczyk, S, Souto-Vilarós, D, McGuire, JA, Renner, SS. 2015 Diversity and clade
519 ages of West Indian hummingbirds and the largest plant clades dependent on them: a 5–
520 9 Myr young mutualistic system. *Biol J Linnean Soc* **114**, 848–859. (doi:10.1111/bij.12476)
521 35. Felsenstein J. 1985 Phylogenies and the comparative method. *Am Nat* **125**, 1–15.
522 36. Paradis E, Claude J, Strimmer K. 2004. APE: Analyses of phylogenetics and evolution in R
523 language. *Bioinformatics*.
524 37. Revell LJ. 2012 Phytools: an R package for phylogenetic comparative biology (and other
525 things). *Methods Ecol Evol* **3**, 217–3223. (doi:10.1111/j.2041-210X.2011.00169.x)

526 38. R Development Core Team. 2016 R: A language and environment for statistical computing.
527 R Foundation for Statistical Computing, Vienna, Austria.
528 39. Vázquez DP, Morris WF, Jordano P. 2005 Interaction frequency as a surrogate for the total
529 effect of animal mutualists on plants. *Ecol Lett* **8**, 1088–1094. (doi:10.1111/j.1461-
530 0248.2005.00810.x)
531 40. Blüthgen N, Menzel F, Blüthgen N. 2006 Measuring specialization in species interaction
532 networks. – *BMC Ecol.* **6**: 9. (doi:10.1186/1472-6785-6-9)
533 41. Fründ J, McCann KS, Williams NM. 2015 Sampling bias is a challenge for quantifying
534 specialization and network structure: lessons from a quantitative niche model. *Oikos* **125**,
535 502–513. (doi:10.1111/oik.02256)
536 42. Vizentin-Bugoni J, Maruyama PK, Debastiani VJ, Duarte, LS, Dalsgaard B, Sazima M.
537 2016 Influences of sampling effort on detected patterns and structuring processes of a
538 Neotropical plant-hummingbird network. *J Anim Eco* **85**, 262–272. (doi:10.1111/1365-
539 2656.12459)
540 43. Dalsgaard B, Schleuning M, Maruyama PK, Dehling DM, Sonne J, Vizentin-Bugoni J,
541 Zanata TB, Fjeldså J, Böhning-Gaese K, Rahbek C. 2017 Opposed latitudinal patterns of
542 network-derived and dietary specialization in avian plant-frugivore interaction systems.
543 *Ecography* **40**, 1395–1401. (doi:10.1111/ecog.02604)
544 44. Dormann CF, Gruber B, Fründ J. 2008 Introducing the bipartite package: analysing
545 ecological networks. *R News* **8**, 8–11.
546 45. McCune B, Mefford MJ. 2006 PC-ORD. Multivariate Analysis of Ecological Data. Version
547 5.10 MjM Software, Gleneden Beach, Oregon USA.

548 46. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 *Mixed effects models and*
549 *extensions in ecology with R*. Springer, New York.

550 47. Martín González AM, Dalsgaard B, Ollerton J, Timmermann A, Olesen JM, Andersen, L,
551 Tossas AG. 2009 The effect of climate on pollination networks in the West Indies. *J Trop*
552 *Ecol* **25**, 493–506. (doi:10.1017/S0266467409990034)
553 48. Rangel TF, Diniz-Filho JAF, Bini LM. 2010 SAM: a comprehensive application for spatial
554 analysis in macroecology. *Ecography* **33**, 46–50. (doi:10.1111/j.1600-0587.2009.06299.x)
555 49. IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY:
556 IBM Corp.
557 50. Vieira MC, Almeida-Neto M. 2015 A simple stochastic model for complex coextinctions in
558 mutualistic networks: robustness decreases with connectance. *Ecol Lett* **18**, 144–152. (doi:
559 10.1111/ele.12394)
560 51. CaraDonna, PJ, Petry, WK, Brennan, RM, Ginnningham, JL, Bronstein, JL, Waser, NM,
561 Sanders, NJ. 2017. Interaction rewiring and the rapid turnover of plant-pollinator networks.
562 *Ecol. Lett.* **20**, 385–394. (doi: 10.1111/ele.12740)

563 52. Solé RV, Montoya JM. 2001 Complexity and fragility in ecological networks. *Proc. R. Soc.*
564 *Lond. B* **268**, 2039–2045. (doi:10.1098/rspb.2001.1767)

565 53. Dunne JA, Williams RJ, Martinez ND. 2002 Network structure and biodiversity loss in food
566 webs: robustness increases with connectance. *Ecol. Lett.* **5**, 558–567. (doi:10.1046/j.1461-
567 0248.2002.00354.x)

568 54. Weinstein, BG, Graham, CH. 2017 Persistent bill and corolla matching despite shifting
569 temporal resources in tropical hummingbird-plant interactions. *Ecol. Lett.* **20**, 326–335. (doi:
570 10.1111/ele.12730)

571 55. Brown JH, Bowers MA. 1985 Community organization in hummingbirds: relationship between
572 morphology and ecology. *Auk* **102**, 251–-269. (doi: 10.2307/4086767)

573 56. Pyke, G. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado:
574 competition and community structure. *Ecology 63,* 555–573. (doi: 10.2307/1938970)

575 57. BirdLife International 2008 Important bird areas in the Caribbean: key sites for
576 conservation. Cambridge, UK: Birdlife International (BirdLife Conservation Series No. 15).
577 58. Janzen DH. 1985 On ecological fitting. *Oikos* **45**, 308–310.
578 59. Agosta SJ, Klemens JA 2008. Ecological fitting by phenotypically flexible genes:
579 implications for species associations, community assembly and evolution. *Ecology Letters*
580 **11**, 1123–1134. (doi: 10.1111/j.1461-0248.2008.01237.x)
581 60. Ollerton J, Erenler H, Edwards M, Crockett R. 2014 Extinctions of aculeate pollinators in
582 Britain and the role of large-scale agricultural changes. *Science* **346,** 1360–1362.
583 (doi:10.1126/science.1257259)
584 61. Sebastián-González E, Dalsgaard B, Sandel B, Guimarães PR. 2015 Macroecological trends
585 in nestedness and modularity of seed-dispersal networks: human impact matters. *Glob Ecol*
586 *Biogeogr* **24**, 293–303. (doi:10.1111/geb.12270)
587 62. Graves, G. 1985 Elevational correlates of speciation and intraspecific geographic variation
588 in plumage in Andean forest birds. *AUK* **102**, 556–579.

589 Table 1. Linear mixed models, analyzing the association between hummingbird resource
590 specialisation *d'* and two types of predictor models: 1) species traits, and 2) local conditions. We
591 also performed a full model including both predictors. In all models we used species identity as a
592 random factor, as for three species the degree of specialisation *d'* was estimated in more than one
593 network. Note that hummingbird specialisation *d'* is only associated to the local conditions. See
594 Table S3 for similar calculations analyzing if the importance of local conditions is mainly due to
595 local abiotic or biotic conditions.

Model	**AIC_c**	**coefficient**	**Std Error**	**CI 95%, lower**	**CI 95%, upper**	**R^2 marginal**	**R^2 conditional**
Species traits	12.033	$+0.048^{NS}$	+0.044	-0.045	+0.140	0.07	0.07
Local conditions	-3.211	+0.12**	+0.022	+0.074	+0.168	0.64	0.73
Full model	1.709					0.66	0.71
species traits		$+0.019^{NS}$	+0.029	-0.046	+0.084		
local conditions		+0.118**	+0.023	+0.069	+0.167		

596 **P<0.001, *p < 0.05, ^{NS} P > 0.05

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598

599 Table 2. Linear mixed models, analyzing the association between hummingbird vulnerability of
600 extinction and two types of predictor models: 1) species traits and 2) local conditions. We also
601 performed a full model including both predictors. In all models we used species identity as a
602 random factor, as for three species the degree of specialisation *d'* was estimated in more than one
603 network. Hummingbird and plant dependencies *R* on mutualism were assigned at random, and
604 hummingbird vulnerabilities to plant extinction, *VE*, were calculated as $VE = PE\ (1 - SE)$. This
605 index captures two components of vulnerability, such that hummingbird species are considered
606 more vulnerable to iterative plant extinctions when they have a higher probability of extinction (*PE*)
607 and when, on average, their extinction occurs early in an extinction sequence ($1 - SE$). We
608 modelled plant extinctions in three orders of deletion: iteratively removing the lowest degree plant
609 species, iteratively removing the highest degree plant species, and at random. Note that
610 hummingbird vulnerability to plant extinction is only associated to the local conditions. See Table
611 S7 for similar calculations analyzing if the importance of local conditions is mainly due to abiotic or
612 biotic conditions. See 'Methods' for details on the modelling, and Table S4 for similar calculations
613 but with the speed of extinction $1 - SE$ as the estimate of species vulnerability. Finally, see Table
614 S5-S6 for similar calculations but assigning plant species dependencies *R* based on their floral
615 phenotype and known insect-pollination visitors.

Model	**AIC_c**	**coefficient**	**Std Error**	**CI 95%, lower**	**CI 95%, upper**	**R^2 marginal**	**R^2 conditional**
Order of deletion: removing species with lowest degree							
Species traits	-10.716	$+0.024^{NS}$	+0.027	-0.035	+0.083	0.01	0.79
Local conditions	-19.800	+0.05*	+0.012	+0.022	+0.075	0.46	0.89
Full model	-13.987					0.44	0.90
species traits		$+0.008^{NS}$	+0.021	-0.041	+0.056		
local conditions		+0.048*	+0.013	+0.020	+0.076		
Order of deletion: removing species with highest degree							
Species traits	-16.367	-0.008^{NS}	+0.022	-0.056	+0.040	0.01	0.74
Local conditions	-16.007	-0.016^{NS}	+0.014	-0.041	+0.020	0.04	0.70
Full model	-10.156					0.03	0.73

species traits		-0.004^{NS}	+0.022	-0.055	+0.046		
local conditions		-0.010^{NS}	+0.015	-0.042	+0.023		
Order of deletion: random removal of species							
Species traits	-46.526	+0.009^{NS}	+0.007	-0.010	+0.027	0.09	0.20
Local conditions	-57.175	+0.018**	+0.004	+0.010	+0.026	0.47	0.86
Full model	-48.917					0.49	0.87
species traits		+0.002^{NS}	+0.007	-0.013	+0.016		
local conditions		+0.018**	+0.004	+0.009	+0.026		

616 **P<0.001, *p < 0.05, ^{NS} P > 0.05

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Fig. 1. (a) Map of the Caribbean Sea, with the Antillean archipelago shown in black and surrounding islands and the American mainland in light grey. The major colonization routes of Antillean hummingbirds are indicated by dark grey arrows, following Abrahamczyk et al. (2015). We show the rate of morphological evolution of hummingbird (b) bill length and (c) body mass through evolutionary time assessed with phylogenetically independent contrasts. The regression line and +/- 95% confidence intervals derived from repeating the analyses across 1,000 post burn-in phylogenies are shown with the solid and dashed lines, respectively. The dark grey shadings reflect the estimated time of hummingbird colonization to the Antilles some 5-9 Mya, following Abrahamczyk et al. (2015). Note that high rates of divergence in hummingbird bill length primarily occurred early in the evolutionary history, before the colonization of the Antilles, while the evolution of body mass differences were more constant through time. The main exception to this general trend was a large recent divergence in body mass between the members of the genus *Eulampis*. The drawing illustrates *Eulampis jugularis* (credit: Pedro Lorenzo).

Fig. 2. The association between hummingbird specialisation *d'* (a, b) and hummingbird vulnerability to plant extinctions *VE* (c, d) with the two main components of 'local conditions', i.e. local abiotic conditions (topography, precipitation and temperature) and local biotic conditions (nectar-food plant richness). High values of the PCA axis 'local environment' reflect topographic complex, high precipitation, and low temperature localities, i.e. Antillean Mountains [18]. The regression line and +/- 95% confidence intervals are shown. Note that some of the data points represent the same hummingbird species observed in several localities; hence we conducted linear mixed models with species identity as a random factor (Table 1, 2).